

# Can dung beetles from the palaeoecological and archaeological record indicate herd concentration and the identity of herbivores?

Smith, David; Nayyar, Kalla; Whitehouse, NJ; Schreve, Danielle ; Thomas, Richard

DOI:

[10.1016/j.quaint.2013.11.032](https://doi.org/10.1016/j.quaint.2013.11.032)

License:

Creative Commons: Attribution (CC BY)

*Document Version*

Publisher's PDF, also known as Version of record

*Citation for published version (Harvard):*

Smith, D, Nayyar, K, Whitehouse, NJ, Schreve, D & Thomas, R 2014, 'Can dung beetles from the palaeoecological and archaeological record indicate herd concentration and the identity of herbivores?', *Quaternary International*, vol. 341, pp. 119-130. <https://doi.org/10.1016/j.quaint.2013.11.032>

[Link to publication on Research at Birmingham portal](#)

## General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

## Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact [UBIRA@lists.bham.ac.uk](mailto:UBIRA@lists.bham.ac.uk) providing details and we will remove access to the work immediately and investigate.



# Can dung beetles from the palaeoecological and archaeological record indicate herd concentration and the identity of herbivores?



David Smith<sup>a,\*</sup>, Kalla Nayyar<sup>a</sup>, Danielle Schreve<sup>b</sup>, Richard Thomas<sup>c</sup>, Nicki Whitehouse<sup>d,e</sup>

<sup>a</sup> Department of Classics, Ancient History and Archaeology, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom

<sup>b</sup> Centre for Quaternary Research, Department of Geography, Royal Holloway, University of London, Egham, Surrey TW20 0EX, United Kingdom

<sup>c</sup> School of Archaeology and Ancient History, University of Leicester, Leicester, United Kingdom

<sup>d</sup> School of Geography, Earth and Environmental Science, Plymouth University, Drake Circus, Plymouth PL4 8AA, United Kingdom

<sup>e</sup> School of Geography, Archaeology & Palaeoecology, Queen's University Belfast, Belfast BT7 1NN, United Kingdom

## ARTICLE INFO

### Article history:

Available online 21 January 2014

## ABSTRACT

We present the results from two analogue studies that examine two aspects of dung beetle populations. Firstly, the degree to which the proportions of dung beetles in terrestrial faunas may reflect herd concentration is assessed by comparing modern sub-fossil faunas retrieved from a range of small ponds at Dunham Massey, Cheshire and Epping Forest in London. These studies suggest that it may be possible to use the proportions of 'dung beetles' recovered to differentiate high from low density grazing pressures in the palaeoentomological and archaeoentomological record.

A second study examines the insect faunas recovered from modern samples of dung from a range of bovids, cervids, suids and equids, chosen to replicate, as closely as possible, Pleistocene taxa. These include the famous Chillingham cattle herd from Northumberland and herds of red deer, wild boar and Konik horses from Kent. When the numbers of individuals and the nature and range of beetles in the whole fauna are considered, it may be possible to differentiate between the dung of a range of different animals. A number of limitations with the present study, their implications and the future potential of this type of study are outlined.

© 2014 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by-nc-nd/3.0/>).

## 1. Introduction

'Dung beetles', taken here to indicate a broad group of different genera whose members are associated with dung (see below), are routinely recovered, sometimes in large numbers, from a range of palaeoecological and archaeological Pleistocene and Holocene deposits. Typically, their presence is only interpreted as providing an indication that grazing and pasture areas were present in the landscape. However, this is a restricted use of a set of insects that have greater interpretative potential (see Robinson, 1983). In this paper, we attempt to establish whether it is possible to broaden the role that 'dung beetles' play in archaeological and palaeoecological interpretations. Dung beetles, *sensu stricto*, are members of the Scarabaeidae family (representing the genera *Geotrupes*, *Onthophagus* and *Aphodius*) which feed, develop, and live in the dung of herbivores (Jessop, 1986). Animal dung is also utilised as a habitat

by a diversity of other beetles such as the Histeridae 'hister beetles', a range of Hydrophilidae (for example *Sphaeridium scarabaeoides* and various *Cercyon* species) and Staphylinidae 'rove beetles'. We include this expanded list of taxa under the heading 'dung beetles' throughout this paper to reflect this wider dung-related community.

This paper will also present the results from two modern analogue studies, compare these with results from a previous study and discuss how 'dung beetles' appear to have had a more significant role to play in the interpretation of sub-fossil insects from a range of Pleistocene, Holocene and archaeological sites than previously suggested.

## 2. Rationale

### 2.1. Showing the potential: research issues

The potential of 'dung beetle' studies is brought into focus by three current archaeological and palaeoecological research issues.

The late Russell Coope identified a large number of 'dung beetles' from numerous Pleistocene sites – especially interglacial sites

\* Corresponding author.

E-mail address: [d.n.smith@bham.ac.uk](mailto:d.n.smith@bham.ac.uk) (D. Smith).

- dating from *circa* one million years ago up to 12,000 years ago. Coope's main emphasis was the use of Coleoptera recovered from these deposits to indicate the nature of climatic conditions and long-term climate change (e.g. Coope, 1961, 1977, 2001, 2010; Atkinson et al. 1987; Elias, 2010). 'Dung beetles' were often used to indicate the presence of herds of grazing animals in the vicinity of the sample site, but the ecology of the species recovered was only investigated when they had specific biogeographical importance. The best example of this is *Aphodius holdereri* (Reitter), which is commonly encountered in cold-climate Pleistocene deposits but which is today limited to a few valleys in Tibet and North-western China (Coope, 1973). However, little emphasis has been placed on the past biogeography and diachronic changes in the abundance of these 'dung beetles' and other species between the various interglacials, interstadials, and stadials throughout the Pleistocene. The detailed ecology of the 'dung beetles' recovered has also remained largely unexplored. Given the recent research interest in the role of herbivores in structuring Pleistocene and Holocene landscapes and their effects on ecosystems, (e.g. Vera, 2000; Gill et al. 2009; Johnson, 2009; Rule et al. 2012; Jeffers et al. 2012), this is potentially an area of significant research interest and one in which fossil beetles can make a meaningful contribution.

In a recent reappraisal of Coope's results from a range of English interglacial sites (Whitehouse et al. 2013, and unpublished data) it is surprising to note that, particularly during the Last (Ipswichian) Interglacial (correlated with Marine Isotope Stage [MIS] 5e 128,000–116,000 years), many of the abundant dung beetle species (for example *Caccobius schreberi* (L.), *Pleurophorus caesus* (Creutz.), *Copris lunaris* (L.), and *Euoniticellus fulvus* (Goeze)) are rare today and primarily associated with sandy and heavily disturbed ground. This strongly suggests that the lowland river valleys in at least this particular interglacial were heavily grazed and that herbivores had a pronounced formative effect on the landscape.

'Dung beetles' have featured in discussions concerning the nature and use of Holocene woodland as well. Many valley fen and riverside deposits from the Early and Middle Holocene contain 'dung beetles' that account for between 5 and 10% of the terrestrial faunas recovered (Whitehouse and Smith, 2010). The presence of these taxa has been used to support the proposition by Frans Vera (2000) that Holocene woodlands contained substantial areas of open grassland and clearings, which were created and maintained by large numbers of grazing herbivores (Svenning, 2002). This conclusion has been recently questioned (Mitchell, 2005; Whitehouse and Smith, 2010) but considerable confusion surrounds the issue of what a 5–10% contribution of 'dung beetles' as a proportion of terrestrial insect faunas actually represents in terms of herbivore herd size and concentration (Smith et al. 2010). A related issue is implied in archaeological discussions that have centred on the use of Neolithic woodland as areas for grazing by domestic animals. Girling (1989) and Robinson (2000) have argued, based on a 10–15% occurrence of 'dung beetles' in the terrestrial fauna at a number of archaeological sites, that herds of domestic animals were 'set loose' to browse in valley woodland. However, both the size of these herds and whether they were associated with domestic stock or wild animals such as deer remains unclear (Whitehouse and Smith, 2010).

Similarly, a number of insect faunas have now been recovered from a range of Late Bronze Age, Iron Age, and Roman field systems in the South East and Midlands of England (e.g. Robinson, 1979, 1993; Lewis et al. 2006; Smith, 2011). Farmoor and Minges Ditches in Oxfordshire (Robinson, 1979, 1993), several sites near Heathrow in Middlesex (Lewis et al. 2006), Little Paxton in Cambridgeshire (Smith, 2011), and Whitmoor Haye in Staffordshire (Smith, 2002) have produced insect assemblages that contain a wide range of Scarabaeidae dung beetles that are common today in

farmed pastures (Jessop, 1986). These taxa, along with members of the wider 'dung beetle community', can account for between 20 and 40% of the terrestrial fauna. However, other field systems, or parts of field systems, from the same period have yielded a very limited range of 'dung beetles' that do not make a substantial contribution to the terrestrial fauna, for example, those from Mount Farm and Barton Court Farm in Oxfordshire (Robinson, 1983). This might imply, as suggested by Robinson (1983), that dung beetle communities could be used to test whether field systems were arable, mixed or mainly used for pasture.

## 2.2. Can the proportions of 'dung beetles' from palaeo- and archaeo-entomological samples indicate the density of grazing?

It has often been assumed that the relative proportions of taxonomic or ecological groups within sub-fossil insect faunas have no real meaning in terms of landscape interpretation (but see Robinson, 1983). At best, the statistics are difficult to interpret directly and, at worst, are thought to have no real meaning. Several pieces of analogue work in the past have clearly outlined the nature of the problem (e.g. Kenward, 1975, 1978, 1982; Smith, 1998). Terrestrial insects, such as 'dung beetles', appear to enter depositional environments (such as bodies of open water) by a number of complex taphonomic routes. This means that their numerical occurrence may not accurately reflect the past contribution that grazing or grassland may have made to an archaeological landscape (Kenward, 1975, 1978). This may be particularly true of the *Aphodius* 'dung beetles', that fly very readily and have a tendency to disperse widely across the landscape as they search for suitable breeding and feeding sites (Kenward, 1975, 1978; Jessop, 1986). One of the key results of Kenward's (1975) 'York drain' experiment was the realisation that potentially large numbers of 'dung beetles' could enter deposits that were a considerable distance away from the nearest area of grazing and pasture. This has led to an unfortunate tendency to think that any consideration of percentage occurrence of 'dung beetles' in archaeological and palaeoecological deposits as being essentially meaningless.

## 2.3. Can the types of 'dung beetles' recovered indicate the types of herbivores present?

There also seems to be an 'unwritten rule' within archaeo-entomology and palaeoentomology that 'dung beetles' cannot be used directly to indicate which species of grazing animal(s) may have been present in the landscape. This is understandable; a quick scan of the literature on dung beetles (Scarabaeidae in particular) suggests that many species do not show a specific preference for the dung of a particular herbivore, but are opportunistic (i.e. the 'host preferences' in Jessop (1986) and Koch (1989) are often non-specific). It has been suggested that this is because dung beetles tend to exploit a resource that is patchy and short-lived (Robinson, 1983). The beetles therefore have to be generalist (polyphagous) in their approach and cannot be over-specific in their preferences. It is often thought, therefore, that the resource partitioning of 'dung beetles' is very broad and has considerable overlap (i.e. Gittings and Giller 1998; Hanski, 1991).

However, recent work has begun to suggest that there may be more general food preferences (trophic habitat separation) shown by the Scarabaeidae in terms of the types of herbivore dung chosen. This is the difference between 'specialist' taxa that might only be associated with a single herbivore and those that favour the dung of a range of browsers (leaf and shoot feeders) but are not interested in the dung of grazers (mainly grass feeders). In essence, these taxa may show a 'broad preference' for the dung of one type, or species

of herbivore over another, if they have a choice (Finn and Giller 2002). Recent field tests have shown that if cattle, sheep and deer are present in the same area, the dung of the three animals will often contain the same range of Scarabaeidae dung beetles, but that one or two particular species will be much more common in one type of dung than the others (Weßmer 1995; Barbero et al. 1999; Dormont et al. 2004, 2007; Gitting and Giller 1988; Finn and Giller, 2002). However, little specific research seems to have been done to see whether there is any broad separation between the dung of ruminants and non-ruminants and between grazers and browsers in terms of the range of associated 'dung beetles'.

Research on Pleistocene insect faunas may also help to clarify this issue. The 'dung beetles' associated with the remains of Pleistocene woolly mammoths (*Mammuthus primigenius* Blumenbach) found at Condovery, Shropshire (Allen et al. 2009) and Lynford, Norfolk (Coope, 2012), with Steppe Mammoth (*Mammuthus trogontherii* Pohlig) at West Runton, Norfolk (Coope, 2000) and with the straight-tusked elephant (*Palaeoloxodon antiquus* Falconer and Cautley) at Aveley, Essex are quite different in their composition from those found in the Holocene. This provisionally suggests that 'dung beetle' populations may, in general, respond to distribution patterns of herbivores, the impact on vegetation and the changing nature of the landscapes herbivores produce.

It is also apparent that geographic factors, season, vegetation cover, local soil condition, humidity, the relative water content of the dung, and the size of the pat and time since defecation may also be determining factors for the range of dung beetles recovered (Koskela and Hanski, 1977; Gittings and Giller 1988; Hanski, 1991; Barbero et al., 1999; Finn and Giller, 2002; Carpaneto et al. 2005). Weßmer (1994, 1995) suggests that the dominant factor is related to season, with other factors having less importance. The lack of understanding concerning the driving factors behind dung beetle occurrence is best articulated by Gittings and Giller (1988, 582), who note that "evidence from the literature on dung beetle preferences for different types of dung is scanty and somewhat contradictory"

### 3. Methods

Here we describe two analogue studies on modern dung beetle populations to with the aim of investigating the potential of these taxa to address the issues raised above. The use of analogue faunas to examine comparable issues is well established and validated within archaeoentomology and palaeoecology (e.g. Kenward, 1975, 1982, 2006; Robinson, 1983; Smith, 1996, 1998, 2000; Smith et al. 1999, 2010). A comparison between the analogue and the past is not about using the data (the insect fauna) as a direct mirror to the past but rather to demonstrate that it is possible to use insect faunas from the modern world to address the archaeological/palaeoecological issue being researched. Though the individual taxa may change between the past and the present, the general nature of the fauna, the effects that circumstances have on that fauna, and the approach taken remain valid (see Smith et al. 2010).

Two types of analogue studies are described here. The fieldwork at Dunham Massey, Cheshire and Epping Forest, London examined the insect faunas from a series of sediment samples taken from ponds in heavily grazed parkland at Dunham Massey; and ungrazed woodland at Epping Forest (Smith et al., 2010). Both studies aimed to examine the extent to which the proportion of 'dung beetles' in the terrestrial faunas reflected the concentration of local herds. The second set of studies described here, from the Wildwood Trust and Stodmarsh NNR in Kent, and Chillingham Park in Northumberland, aim to examine the extent to which the recovered 'dung beetles' varied between the dung of different species of large mammals.

Differences in methodology at each of the study sites reflect different research goals of the overall projects at each site (see Smith et al. 2010); issues of inter-site comparability are discussed at length below. The locations of the sites used in this study are indicated in Fig. 1.

#### 3.1. Fieldwork and investigations at Dunham Massey and Epping Forest

The Old Park at Dunham Massey, Cheshire, is a 101 ha deer park that is grazed by a herd of around 250 fallow deer (*Dama dama* (L.)). Epping Forest (London Borough of Epping Forest District) is a 2430 ha area of dense deciduous woodland interspersed with open grassy 'plains' and home to a population of around 500 individuals of muntjac deer (*Muntiacus reevesi* (Ogilvy)) and fallow deer along with a small seasonal herd of cattle (*Bos taurus* L.). Recent sediments (probably representing less than ten years of accumulation) were sampled from the bottom of the ponds at both sites using a Ponar grab sampler. Five samples were taken from each of four ponds at Dunham Massey and five samples from four ponds at Epping Forest, representing a total of 40 samples in total. A volume of around ten litres of sediment was sampled from each of the individual sampling sites.

Insect remains were extracted from the material using the standard procedure of paraffin flotation outlined by Kenward et al. (1980). The aim was to recover the sub-fossil fauna in such a way that sampling and depositional history would match similar water-lain deposits in the archaeological and palaeoecological record. The coleopterous (beetle) faunas recovered were identified using a range of biological keys and by direct comparison to the Gorham and Girling collections housed at the University of Birmingham.

The insects recovered from the ponds at Dunham Massey and Epping Forest were assigned to a range of ecological groups based on the scheme outlined by Robinson (1981, 1983), which includes one that is exclusive to 'dung beetles' (group 'df' – in Smith et al. 2010). The ecological significance of the overall results from the sites is explored in Smith et al. (2010).

#### 3.2. Field work and investigations at the Wildwood Trust, Stodmarsh and Chillingham

##### 3.2.1. Wildwood Trust

The Wildwood Trust, Kent is a 40 ha zoological park that contains around 300 specimens of a range of species that were either present themselves in the Late Pleistocene and Early Holocene in Britain or represent close relatives of now-extinct forms. These include Konik horses (*Equus caballus* (L.)) (the result of an attempt to breed back to the European tarpan (*Equus ferus ferus* (Boddaert)) in the latter part of the 18th century), red deer (*Cervus elaphus* (L.)) and wild boar (*Sus scrofa* (L.)). These animals are allowed to roam in large wooded enclosures and are fed with a range of prepared and commercial feeds.

Sampling at Wildwood occurred late in July 2010. Four samples of dung were taken each from the Konik, red deer and wild boar enclosures. The material was usually around 3–4 L in volume. The dung was placed in a bucket of water and the larger organic component was kept under the surface using a 4 cm mesh sieve. The 'dung beetles' were collected as they floated to the surface of the water in the bucket. This process was continued, with periodic stirring of the material, until all live insects were extracted.

##### 3.2.2. Stodmarsh

Stodmarsh is a 165 ha National Nature Reserve (NNR) located in the Stour Valley in north Kent. It contains a mix of grazing marsh, meadowlands, reed bed and open water crossed by a maze of



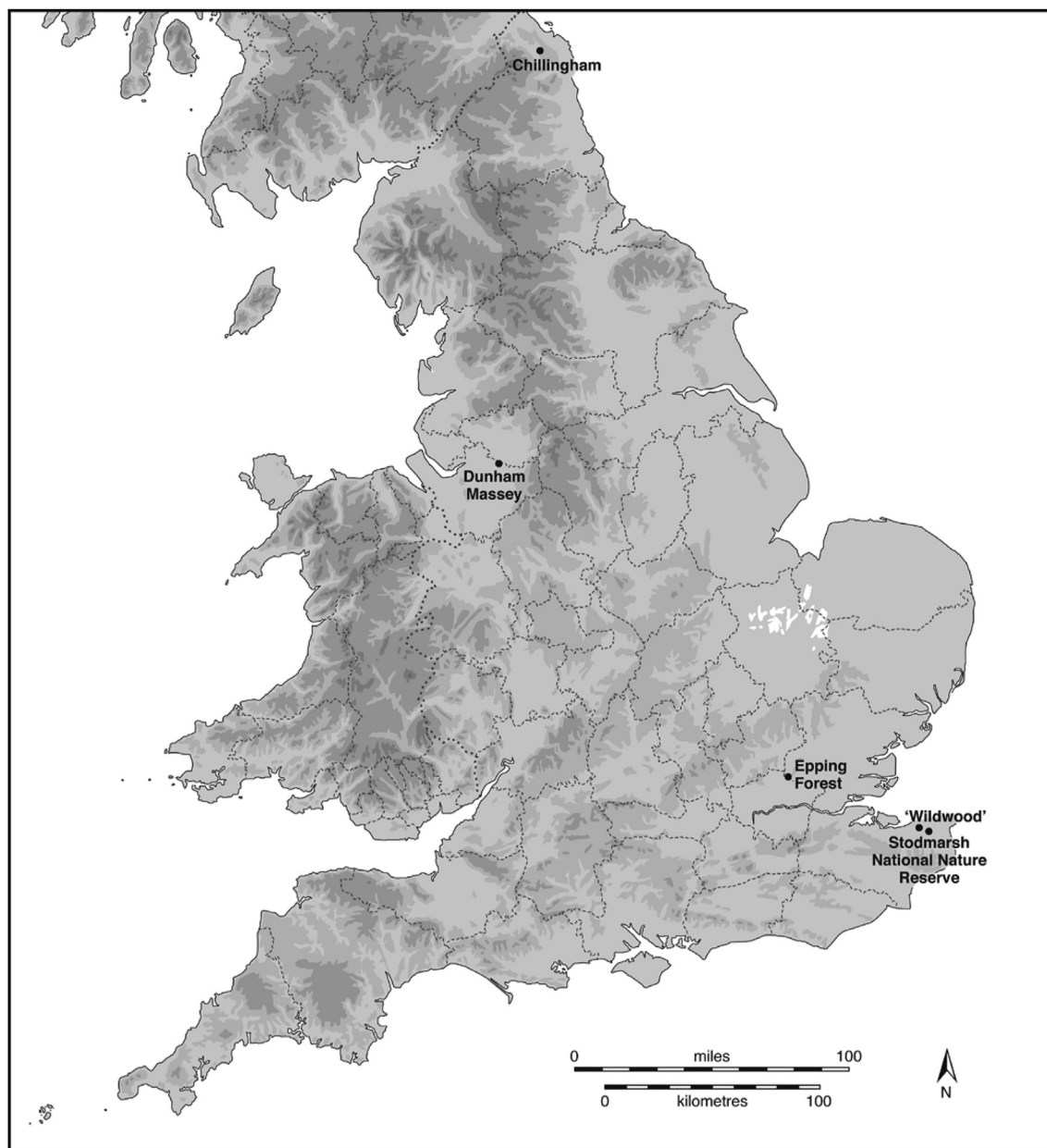


Fig. 1. Map of the sites discussed.

vegetationally diverse ditches. Today, the wet grassland is managed for conservation grazing purposes by a herd of 15–20 Konik horses owned by the Wildwood Trust. The welfare of the horses is monitored but no supplementary feeding occurs.

Five samples of dung were collected from the Konik herd in early July 2010 and were also around 4–5 L in volume. These were washed, dried and then sorted by hand to extract the dead insects prior to identification.

### 3.2.3. Chillingham

Chillingham Park, Northumberland, is home to the Chillingham 'Wild White Cattle'. These cattle are believed to be descendants of a herd of domestic cattle that was brought together in the late medieval period. They are distinct from modern cattle both in form and behaviour and are widely regarded as an archaic and 'unimproved' breed. Today, the herd is enclosed in a 130 ha 'pasture

woodland' enclosure on the estate. Though their welfare is monitored, they are left to graze and organise their herd structure with minimal human interference. Samples of dung from the Chillingham herd were collected in late August 2011 and were around 1–2 L in volume.

Pictures of the 'donors' of the sampled material are shown in Fig. 2 and of the types of dung sampled in Fig. 3.

## 4. Results

### 4.1. Proportions of 'dung beetles' from Dunham Massey and Epping ponds

The beetle fauna recovered from the ponds at Dunham Massey and Epping Forest were presented in Table 3 in Smith et al. (2010). Fig. 4 presents the proportions of 'dung beetles' as a percentage of



Fig. 2. Animals that provided dung samples (a) cattle at Chillingham, (b) Konik at Stodmarsh, (c) Red deer at Wildwood, (d) wild boar at Wildwood).

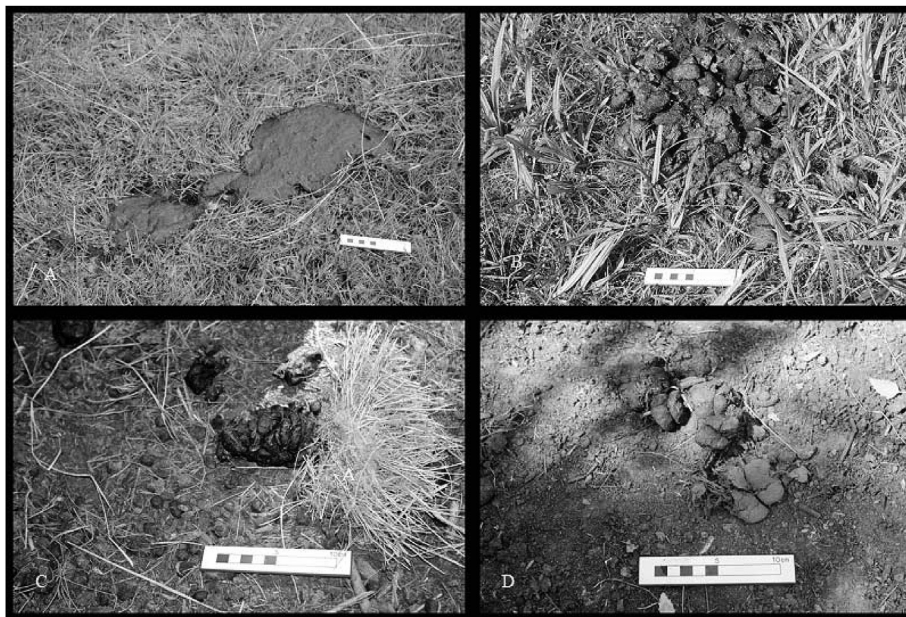


Fig. 3. Examples of animal dung (a) cattle dung, (b) Konik dung, (c) red deer dung, (d) wild boar dung (scale = 10 cm).

the terrestrial fauna recovered from these pond samples. The 'dung beetles' recovered at both sites are from a relatively limited range of species. These are mostly a number of hydrophilids such as *Cercyon impressus*, *Cercyon haemorrhoidalis*, *C. atricapillus* and *C. analis*. In terms of Scarabaeidae, the ponds at Dunham Massey produced comparatively more individuals than those at Epping, mainly the 'generalist' *Aphodius sphacelatus*. Between 3 and 16 individuals of dung beetles were recovered from the individual ponds at Dunham Massey. At Epping, the Scarabaeidae fauna is much smaller in number (between 1 and 5 individuals per pond) but contained one individual of *Aphodius zenkeri* (from Alder pond), which is almost exclusively associated with dung in woodland (and here, in deer dung) (Jessop, 1986; Koch, 1989; Weßmer 1995). Generally, the 'dung beetles' account for a higher proportion of the terrestrial

fauna at Dunham Massey (15.8% at Island Pond, 7.6% at Old Man's Pond and 10.6% at Smithy Pond) than at Epping (4.2% at Alder Pond, 0.6% at Baldwin's Pond, 2.8% at Fairmead Pond and 1.9% at Lost Pond).

#### 4.2. Dung pat beetles from Wildwood, Stodmarsh and Chillingham

The beetle fauna recovered from the sampled dung at Wildwood, Stodmarsh and Chillingham is summarised in Tables 1 and 2 and Fig. 5. The nomenclature and taxonomic order follows Lucht (1987). The numbers in the table represent the number of individuals (MNI) recovered. Fig. 5 displays the number of individuals and the number of taxa recovered from the dung pats. Table 2 is a summary of the occurrence of the main families of 'dung beetles'

**Table 1**

The coleopterous fauna recovered from the animal dung (nomenclature follows that of Lucht 1979).

Site	Ecological codes	Wildwood								Chillingham								Stodmarsh								
Herbivore		Konik				Boar				Deer				Cattle								Konik				
Sample		1	2	3	4	Pru 2	Pru 1	Boris 1	Boris 2	1	2	3	4	1	2	3	4	5	6	1	2	3	4	5		
<b>Hydraenidae</b>																										
<i>Helophorus</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–		
<b>Hydrophilidae</b>																										
<i>Sphaeridium scarabaeoides</i> (L.)	rf	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	6	6	–	–	11	–	2	8		
<i>Sphaeridium lunatum</i> F.	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1		
<i>Cercyon impressus</i> (Sturm)	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	36	–	–	18	1	–	–		
<i>Cercyon haemorrhoidalis</i> (F.)	rf	–	4	6	4	–	–	–	3	1	–	–	–	–	–	–	–	1	–	10	1	89	45			
<i>Cercyon melanocephalus</i> (L.)	rf	4	1	20	4	–	–	–	–	–	–	–	–	19	13	–	2	4	–	–	19	–	2	7		
<i>Cercyon quisquilius</i> (L.)	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	79	–	13	14		
<i>Cercyon pygmaeus</i> (Ill.)	rf	–	6	3	2	–	–	1	–	–	–	–	–	–	–	–	14	3	–	8	200	–	35	81		
<i>Cryptopleurum minutum</i> (F.)	rf	22	11	6	3	1	–	1	1	–	–	–	–	–	–	–	–	–	1	1	–	–	1	6		
<b>Clamidae</b>																										
<i>Clambus punctulum</i> (Beck)		–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<b>Ptiliidae</b>																										
Ptiliidae Gen. & spp. indet.	rt	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	18	10	3	–	1		
<i>Ptenidium pusillum</i> (Gyll.)	rt	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Acrotrichis sericans</i> (Heer)	rt	–	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Acrotrichis</i> spp.	rt	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<b>Staphylinidae</b>																										
<i>Megarthus depressus</i> (Payk.)		2	1	1	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	1	–	–		
<i>Omalium italicum</i> Bernh.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–		
<i>Oxytelus laqueatus</i> (Marsh.)	rf	5	2	2	3	–	–	–	3	–	–	–	–	10	10	–	18	7	6	1	1	–	–	1		
<i>Oxytelus sculpturatus</i> Grav.	rt	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Oxytelus nitidulus</i> Grav.	rt-d	4	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	3	5	–	10	8			
<i>Oxytelus complanatus</i> Er.	rt	–	–	–	–	–	–	5	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–		
<i>Oxytelus tetracarinaratus</i> (Block)	rt	50	14	13	5	–	–	7	1	–	–	–	–	–	1	–	12	–	15	30	5	6	4	8		
<i>Platystethus arenarius</i> (Fourc.)	rf	1	–	–	1	–	–	5	–	–	–	–	–	–	1	–	7	3	–	–	–	–	–	1		
<i>Stiliculus orbiculatus</i> (Payk.)		–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Xantholinus linearis</i> (OL.)	rt	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Philonthus cruentatus</i> (Gm.)		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–		
<i>Philonthus splendens</i> (F.)	rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–		
<i>Philonthus fimetarius</i> (Grav.)	rf	1	–	1	2	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Philonthus marginatus</i> (Müll.)	df	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–		
<i>Philonthus</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–		
<i>Tachinus rufipes</i> (Geer.)	u	11	–	6	9	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Leucoparyphus silphoides</i> (L.)	rt	6	1	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Autalia rivularis</i> (Grav.)		3	1	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Aleochara lanuginosa</i> Grav.		2	–	–	–	3	1	1	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–		
<i>Aleochara bipustulata</i> (L.)		–	–	–	–	10	5	11	3	–	1	–	–	–	–	–	–	–	3	–	–	–	1	–		
<i>Aleochara</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	1	–	–		
<i>Aleocharinidae</i> Genus & spp. Indet.		16	31	27	16	2	2	4	9	–	–	–	–	7	7	–	–	–	1	1	3	–	–	–		
<b>Cucujidae</b>																										
<i>Monotoma brevicollis</i> Aubé		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–		
<b>Cryptophagidae</b>																										
<i>Telmatophilus typhae</i> (Fall.)		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–		
<b>Endomychidae</b>																										
<i>Mycetaea hirta</i> (Marsh.)	rd-h	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1		
<b>Scarabaeidae</b>																										
<i>Onthophagus similis</i> (Scriba)	oa-rf	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Aphodius erraticus</i> (L.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	2	–	2		
<i>Aphodius haemorrhoidalis</i> (L.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1		
<i>Aphodius rufipes</i> (L.)	oa-rf	–	–	–	–	3	–	–	–	–	–	–	3	4	–	2	–	1	–	–	–	–	–	–		
<i>Aphodius zenkeri</i> Germ.	oa-rf	–	–	–	–	–	–	9	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Aphodius equestris</i> (Panz.)	oa-rf	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<i>Aphodius contaminatus</i> (Hbst.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–		
<i>Aphodius sphacelatus</i> (Panz.)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–		
<i>Aphodius prodromus</i> (Brahm)	oa-rf	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–		
<i>Aphodius fimetarius</i> (L.)	oa-rf	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1		
<i>Aphodius rufus</i> Moll.	oa-rf	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
<b>Curculionidae</b>																										
<i>Barypeithes sulcifrons</i> (Bohe)	oa	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
Total number of individuals		131	76	95	57	26	10	47	28	4	2	0	0	37	33	0	70	63	26	68	366	17	162	186		
Number of taxa		15	12	16	15	10	5	12	9	4	2	0	0	7	7	0	11	8	7	11	14	10	11	16		

Ecological coding follows that of Kenward and Hall 1995. oa = usually not associated with settlement. rf = rotting foul often animal dung. rt = rotting plant material. rd-h = associated with drier organic material in settlement.

**Table 2**

Summary of the occurrence of the main families of the beetle faunas recovered from Wildwood, Stodmarsh and Chillingham. Underlined species seem particularly significant.

'Donor' species	Site	Hydrophilidae	Staphylinidae	Scarabaeidae
Horse	Wildwood	<i>Cercyon haemorrhoidalis</i> <u><i>C. melanocephalus</i></u> <i>C. pygmaeus</i>	<u><i>Oxytelus tetracarinatus</i></u> <u><i>O. laqueatus</i></u> <i>Tachinus rufipes</i> <i>Autalia rivularis</i> <i>A. langinosa</i>	X
	Stodmarsh	<i>Sphaeridium scarabaeoides</i> <i>Cercyon impressus</i> <u><i>C. haemorrhoidalis</i></u> <u><i>C. quisquilius</i></u> <u><i>C. melanocephalus</i></u> <u><i>C. pygmaeus</i></u>	<u><i>Oxytelus nitidulus</i></u> <u><i>O. tetracarinatus</i></u> <i>Aleochara bipustulata</i>	
Cattle	Chillingham	<i>Sphaeridium scarabaeoides</i> <u><i>Cercyon impressus</i></u> <u><i>C. melanocephalus</i></u> <u><i>C. pygmaeus</i></u>	<u><i>Oxytelus tetracarinatus</i></u> <u><i>O. laqueatus</i></u> <u><i>Platystethus arenarius</i></u> <i>Philonthus marginatus</i> <i>P. splendens</i>	<i>Aphodius rufipes</i> <i>A. prodromus</i>
Red Deer	Wildwood	X	X	X
		X		
Boar	Wildwood	X	<i>Oxytelus complanatus</i> <i>O. tetracarinatus</i> <i>Aleochara lanuginosa</i> <u><i>A. bipustulata</i></u>	<u><i>Aphodius zenkeri</i></u> <i>A. equestris</i>

recovered from the four main types of animal dung. Species that are underlined appear to represent a dominant aspect of the faunas.

#### 4.2.1. Chillingham: cattle dung

Fig. 5 suggests that cattle dung produced relatively lower numbers of individuals compared with horse dung. However, the cow pats at Chillingham were very flat and thin compared to the

more substantial 'piles' of horse dung sampled at Wildwood and Stodmarsh (Fig. 3). As a result, at Chillingham it was only possible to collect samples of dung that were around a quarter of the volume compared to those collected from the other species. If similar volumes of cattle dung had been collected, the numerical size of the beetle fauna would probably have been comparable to the dung of Konik horses at Wildwood and Stodmarsh.

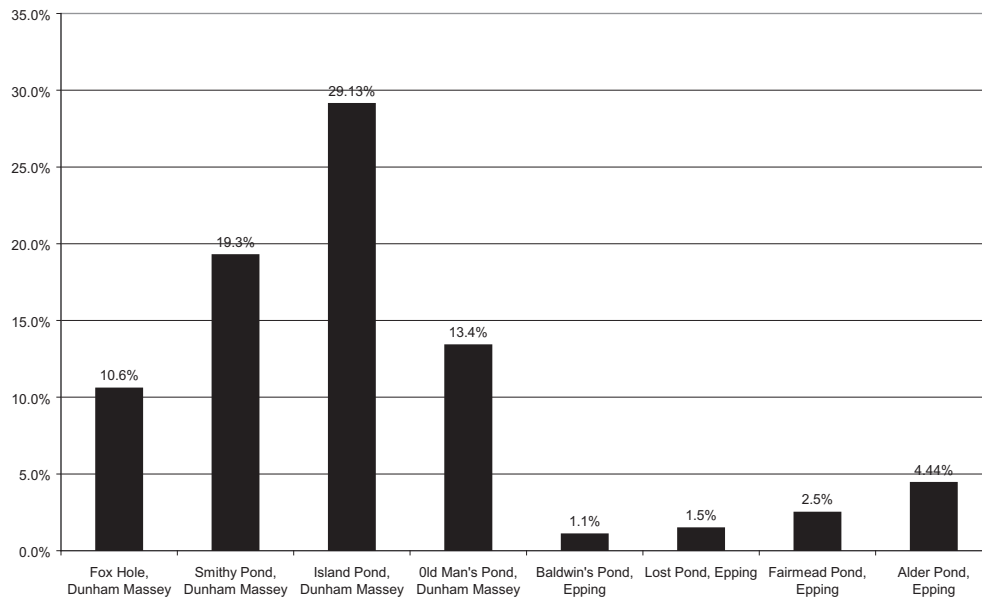


Fig. 4. The relative proportions of taxa associated with dung (df) from Dunham Massey and Epping (see Smith et al. 2010 for full data).



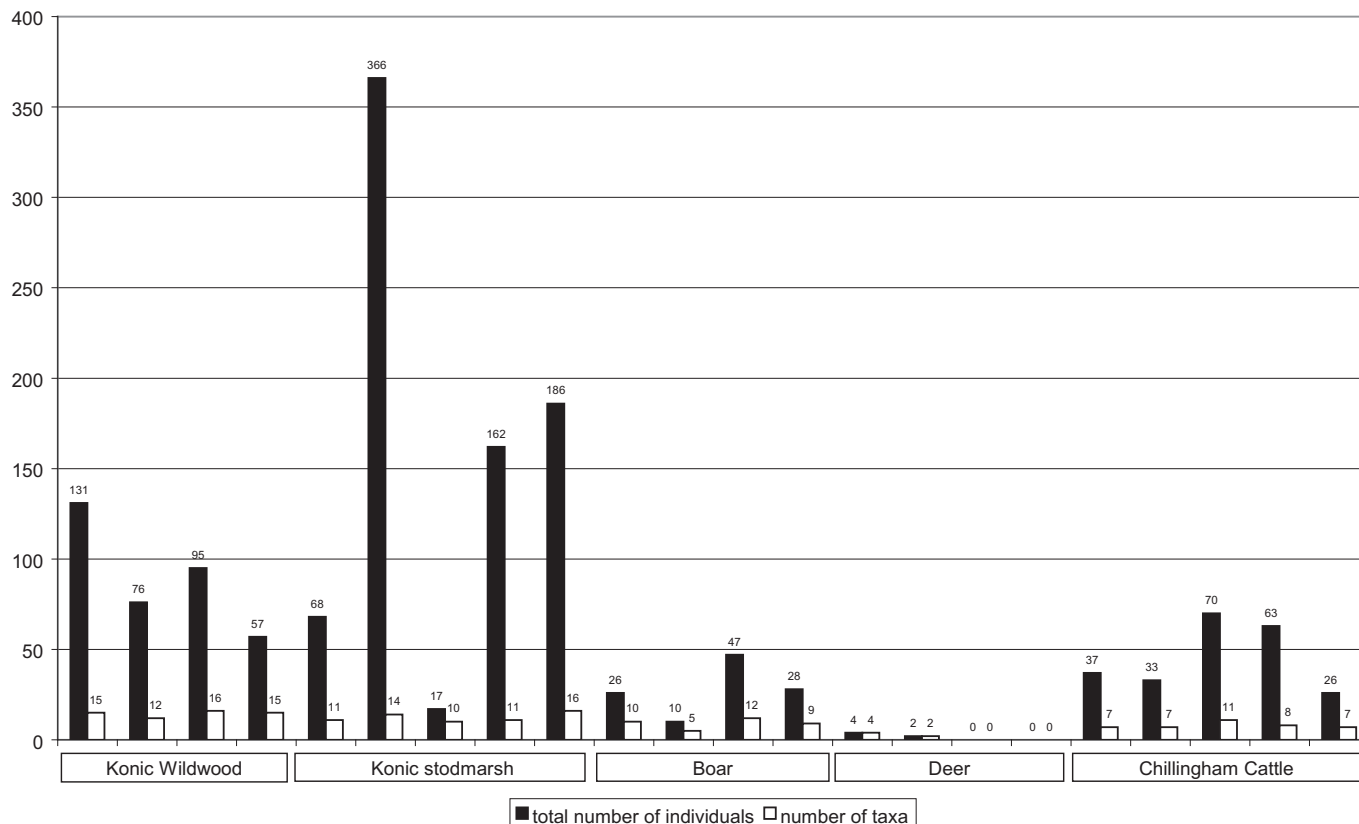


Fig. 5. Number of individuals and number of taxa from the dung pats.

The beetles recovered from the cattle dung from Chillingham could be considered an example of a 'classic dung beetle fauna'. *Sphaeridium scarabaeoides* is usually exclusive to animal dung, often that of cattle (Hansen, 1987). However, it can be found in a range of very fluid and wet organic matter such as stabling material (Hansen, 1987; Koch, 1989). The three species of *Cercyon* recovered (*Cercyon impressus*, *Cercyon melanocephalus* and *Cercyon pygmaeus*) are often associated with animal dung, but also can occur in a much wider range of wet and decaying plant materials (Hansen, 1987; Koch, 1989). *Oxytelus laqueatus* and *Platystethus arenarius* are almost exclusive to animal dung, often occurring in very large numbers (Tottenham 1954; Lott, 2009). *Philonthus marginatus* and *Philonthus splendens* are common in, though not exclusive to, animal dung that has become quite dry (Koch, 1989). The two Scarabaeidae dung beetles recovered from the cattle dung, *Aphodius rufipes* and *Aphodius prodromus*, are considered to be very generalist in their preferences and are quite common in modern animal dung (Jessop, 1986). Drawing upon archaeological data, Carrott and Kenward (2001) and Kenward et al. (2004) have suggested that both of these *Aphodius* species were likely able to breed in the wetter and fouler parts of human habitation.

#### 4.2.2. Wildwood and Stodmarsh: Konik dung

The Konik horse dung, sampled from both Wildwood and Stodmarsh, produced a large number of individuals per dung pat but these 'dung beetles' are derived from a comparatively restricted range of insects. This range of species, to some extent, departs from the 'classic community' seen in the Chillingham cattle dung. Again, relatively large numbers of *Cercyon* beetles were recovered, with *Cercyon quisquilius* occurring in very large numbers at Stodmarsh. *C. quisquilius* is common in animal dung but Hansen (1987) and

Koch (1989) suggest that it is also abundant in wet decaying vegetation. Except for *Oxytelus laqueatus*, the staphylinids recovered are quite different in their nature to those seen in the cattle dung. *Oxytelus tetracaratus*, *Oxytelus nitidulus*, *Tachinus rufipes*, *Autalia rivularis* and *Aleochara lanuginosa* are all species that are common in loose structured and decaying plant materials, such as compost heaps and stabling waste, as well as in animal dung (Tottenham 1954; Koch, 1989; Lott, 2009). Many of these taxa are also commonly found in archaeological contexts where they are again associated with loose structured waste materials and stabling matter (Kenward and Hall, 1995, 1997; Smith, 2000; Carrott and Kenward, 2001). Welch (1997) suggests that *Aleochara bipustulata* (recovered from Stodmarsh) is usually associated with sheep, horse and dog dung. No Scarabaeidae dung beetles were recovered from the Konik dung at Wildwood. Two *Aphodius* dung beetles were found in small numbers from the Konik dung at Stodmarsh. *Aphodius erraticus* and *Aphodius haemorrhoidalis* are often associated with horse, sheep and to a lesser extent cattle dung in open areas (Jessop 1987).

#### 4.2.3. Wildwood: red deer dung

The four samples of deer dung from Wildwood produced a very small fauna of insects with only one taxa, *Aphodius rufus*, specifically associated with animal dung.

#### 4.2.4. Wildwood: wild boar dung

Wild boar dung also produced comparatively low number of individuals compared to the horse and cattle dung. No hydrophilids were recovered. The staphylinids were dominated by *Aleochara bipustulata*, which tends to be associated with the drier dung of dog, sheep and horse (Welch, 1997). *Aphodius zenkeri* was recovered in relatively large numbers from the wild boar dung and is

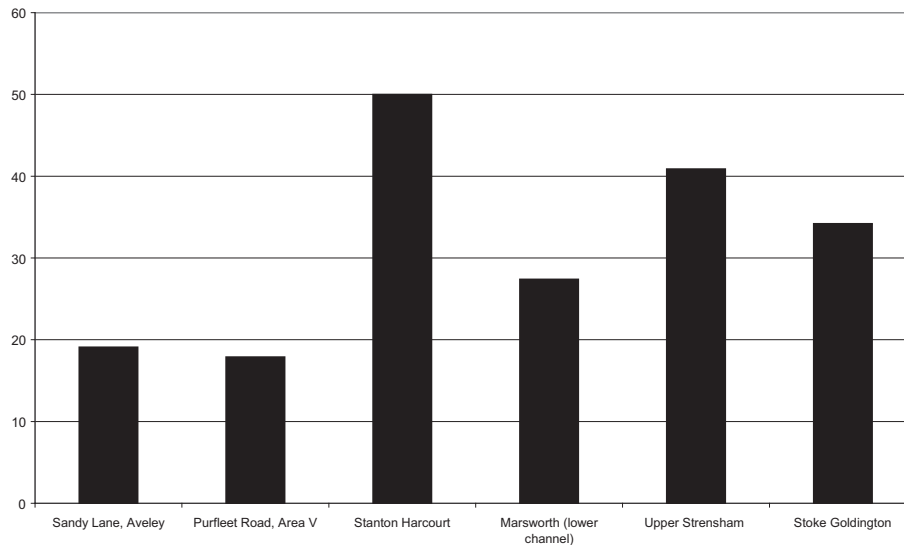


Fig. 6. Proportions of dung beetles from a range of terrestrial insect faunas from a range of MIS 7 sites.

frequently associated with dung, often deer, in woodland (Weßmer 1995), as is *Aphodius equestris* (Jessop, 1986).

## 5. Discussion

### 5.1. Can the proportions of 'dung beetles' in palaeo- and archaeo-entomological faunas indicate herd concentration?

The modern analogue work from the ponds at Dunham Massey and Epping suggests that the proportions of 'dung beetles' in terrestrial faunas can separate landscapes where the level of grazing is relatively low from those where it is relatively high and where animals are heavily concentrated. If the data presented here are taken at face value, it might be suggested that where 'dung beetles' (of all types) account for <10% of the palaeoecological terrestrial fauna, we are most likely dealing with low densities of animals spread widely across the landscape. Conversely, values of >20% are suggested to indicate high densities of grazing animals, or at least local herd concentrations (Smith et al. 2010). These data appear to support the conclusions reached by Robinson (1983) who used the results of a number of pit fall and sweeping surveys to suggest that there was an intrinsic difference in the insect faunas from pasture on one hand and arable fields on the other.

If this 'rule of thumb' is accepted, this leads to a number of interesting conclusions about past insect faunas and what they might indicate about herd densities and strategies. Though the proportions of 'dung beetles' in Pleistocene deposits have not been routinely calculated, a simple scan of the available species lists (all contained in Buckland and Buckland, 2006) suggests that they are often a dominant part of these faunas. This can be seen in some recent work on the insect fauna from the Sandy Lane and Purfleet Road sites at Aveley, Essex (Schreve et al., unpublished data) which date to the penultimate interglacial (MIS 7 c. 240–200 ka) (Schreve, 2004). Dung beetles were relatively common in the terrestrial faunas at both sites with values close to 20% (see Fig. 6) (Schreve et al., unpublished data). These proportions are similar to those recovered from the modern ponds at Dunham Massey, suggesting that large herbivores must have been as dominant a part of the Pleistocene landscape as they are in this modern deer park. A comparison with other MIS 7 sites (Whitehouse et al. 2013; unpublished data) (Fig. 6) indicates that in a range of deposits, often

associated with the remains of large herbivores, dung beetles can account for up to 50% of the insect faunas recovered. At a minimum, this at least implies sizeable herds of large grazing animals present and highlights the important role that large herbivores must have played in shaping these interglacial environments.

Similar arguments could also be made for the issue of Holocene woodland grazing by domestic livestock. In the majority of the Holocene sites examined by Whitehouse and Smith (2010), 'dung beetle' values are routinely below 20% of the terrestrial fauna. This perhaps indicates that 'Neolithic grazing' of domestic livestock was limited in extent or, if the 'dung beetles' were associated with the dung of wild animals, these were present in concentrations more similar to those at Epping rather than in the deer park at Dunham Massey. If this proposition holds true, it may be possible to use the proportions of 'dung beetles' in the terrestrial fauna to identify which archaeological landscapes and field systems from later pre-history were associated with domestic livestock and those that were intensively grazed. For example, the late 2nd to 4th century AD riverside 'ladder' field system at Little Paxton, Cambridgeshire, produced six insect faunas for which 'dung beetles' accounted for between 22 and 25% of terrestrial taxa recovered (Smith, 2011). This clearly suggests that this field system was pastoral rather than arable. A similar approach was also taken by Robinson in his comparative survey of a number of Iron Age insect faunas from the Thames Valley (Robinson, 1983).

Despite the evident potential of the approach taken here, conclusions must be drawn with care and a number of recommendations for future research can be made. The data concerning relative proportions of dung beetles as part of terrestrial faunas are only derived from a limited number of samples from two modern study locations (Dunham Massey and Epping). Furthermore, one of these (Dunham Massey) is a deer park where the concentration of animals may be unnaturally high. A wider range of sites, with different concentrations of animals, thus needs to be investigated before firmer conclusions can be drawn. At present these data are also solely based on a study of one large animal – fallow deer. The same type of experiment should consequently be repeated with a wider range of animals including domestic livestock as well as 'wild' animals.

Taphonomic considerations and how the archaeological and palaeoecological records form should also be taken into account. In

this study the samples were deliberately taken from small, still-water ponds. The majority of Pleistocene and Holocene sites, however, are associated with river systems, alder carrs, raised bogs and, in the case of Late Holocene archaeological sites, ditches in field systems where depositional patterns are less clear and largely unstudied.

Several issues concerning sampling also need to be investigated further. 'Dor beetles' (*Geotrupes* spp.) were absent from these faunas. One of the reviewers of this paper and Weßmer (1995) suggest that *Geotrupes*, *Onthophagus*, and other tunnellers, rapidly retreat into their burrows when the dung is disturbed leaving only a few seconds to collect them. This suggests that the strategies used to collect the 'whole' fauna from the dung affects species representation needs to be evaluated.

## 5.2. Can we use dung beetle assemblages to identify specific animals in the landscape?

The results presented here suggest that it is possible to distinguish four separate large mammal species on the basis of beetle assemblages associated with their dung. It is also clear that cattle and horse dung produce much larger populations of 'dung beetles' than either deer or wild boar. Furthermore, there appear to be intrinsic differences in the major groupings of beetles recovered, particularly where the staphylinids and scarabaeids are concerned. This raises the possibility that grazers (grass and herb feeders such as horse and cattle) can be separated from browsers (deer) and that both of these can be differentiated from omnivores (wild boars). Boar dung in particular has been reported to be particularly unattractive to Scarabaeidae (Barbero et al. 1999).

The results of the present study may reveal why this occurs. Both the Chillingham cattle and the Konik horses in this survey produced very large, wet and loosely-structured pats. In contrast the deer and wild boar dung samples although fresh, were dry to the point of near desiccation, very compacted and each 'pat' or 'pellet' very small in volume (Fig. 3). This is seemingly not related to a straightforward difference between monogastrics (e.g. horse, wild boar) and ruminants (cattle, deer) but reflects the overall efficiency of each taxon in extracting nutrients and water from their food source. Dryness of dung has been shown by experiments in Africa to be a limiting factor in terms of the number of Scarabaeidae dung beetles recovered (Gittings and Giller, 1998). This is specifically related to 'pellet size', suggesting that larger faecal masses desiccate at a slower rate. Dryness was cited as a factor in determining dung beetle populations in dog excrement in Rome (Carpaneto et al. 2005). One key aspect of this phenomenon is that both dry and very fluid materials prevent the oviposition of eggs by Scarabaeidae (Gittings and Giller, 1998). Gittings and Giller (1998) have also suggested that the volume and fragment size of fibre in the pats may also influence what can live and breed in dung. This may partially explain the difference in the community of beetles recovered between the Chillingham cattle and the Konik horses seen here. In Fig. 3, it is apparent that the plant materials in the Konik dung is very bulky, fibrous and less processed, as is typical for a monogastric animal and in contrast with cattle where plant remains are finely milled in a process characteristic of rumination. Similar conclusions were also reached by Weßmer (1995) who identified distinct differences in the fauna of 'dung beetles' recovered from sheep pellets and cow pats.

As with the studies reported above, conclusions must be drawn with care on the basis of a relatively modest data set but again a number of recommendations for future study can be made. For example, recordings of relative size, weight, volume, moisture and relative fibre content of dung pats could be taken. In addition, it should be borne in mind that none of the sampling sites represent

completely 'wild' conditions. Although the animals were kept in large enclosures, they were not free to roam and, at the Wildwood Trust, part of the Koniks' diet comes from prepared animal feed as well as graze. This study also takes no account of factors such as variation in seasonality or the interval since defecation. These have all previously been identified as important factors in shaping the dung beetle community (Koskela and Hanski, 1977; Hanski, 1991; Weßmer, 1994, 1995; Gittings and Giller, 1998). Lastly, a much larger number of dung pats taken from a wider range of landscapes should be examined in future. Particularly important in terms of these analogues, especially those from the woodland in Epping and the Wildwood Trust, are the observations of Koskela and Hanski (1977) and Weßmer (1995) that suggest cow dung in woodland contained both a smaller population and diversity of 'dung beetles' than those from grassland.

Lastly, the modern insect faunas were recovered directly from dung pats. In contrast, most archaeoentomological and palaeoecological faunas come from former water bodies into which terrestrial insects have been washed in, been accidentally incorporated or occur as part of 'flight faunas' (*sensu* Kenward, 1978). We only are aware of one example from the archaeological record where the insects and plants sampled appear to have come *directly* from a dung pat. This is a closely-sampled deposit from the outer ditch at Banbury Castle dating to 1640–1778 AD (Smith and Smith, 2009 unpublished data). A sub-sample taken for plant macrofossils contained a superabundance of seeds from *Campanula* cf. *latifolia* (giant bell flower). The same sub-sample also contained large numbers of puparia of flies in the families Limosinidae and Sepsidae. These are typically associated with animal dung and human excrement (Smith, 1989). This combination of biological remains was interpreted as representing a single cow pat, which contained the remnants of a giant bell flower that had fallen directly into the ditch (Smith and Smith, 2009 unpublished report).

Though a larger study, similar to the case study described above, that examines beetles from dung pats might reinforce an association between specific herbivores and 'dung beetles', an additional component to this study would be needed in order to apply these results directly to the archaeological and palaeoecological record. 'Ponar sampling' of a series of nearby ponds or ditches in the same area as any 'dung pat' could be undertaken to produce data that are directly comparable to the archaeological and palaeoecological record.

## 6. Conclusions

The initial investigations of various herbivore dung pats described above have demonstrated the potential of 'dung beetles' as a proxy for answering questions about past herbivore presence, numbers and grazing intensity. This can be applied to a range of Pleistocene and Holocene deposits, even where no animal bones have been found.

However, the studies described above have, in the way most modern analogue studies tend to do, raised a number of additional questions and concerns that require further exploration. The ability of the proportions of dung beetles in terrestrial insect faunas to act as a direct indicator of herd concentration and density needs further analogue testing. A more comprehensive study would need to examine more samples taken from a wider range of environments with differing levels of herd density and composition than that undertaken here. Further research would need to consider variations in season, pat composition and so forth, in addition to the type(s) of animal concerned. Any further study would need to examine the dung of herds that are freer roaming than some of the animals examined here. Finally, as indicated above, the analogue study also should include samples taken from small water bodies

near grazing herds of varying size in order to make the results directly comparable to the palaeoenvironmental and archaeological records.

## Acknowledgements

Permission to take samples from Dunham Massey was obtained from Andrew Wylie (National Trust) and at Epping by both Jeremy Dagley and Imogen Wilde (Corporation of London) who also provided field assistance. Permission to obtain samples at the Wildwood Trust came from Peter Smith (chief executive) Field assistance and advice came from Anne Riddell (Head of Education) and Paul Wirdnam (Head Keeper) at the Wildwood Trust and Stodmarsh NNR. Both Chris Leyland and Richard Marsh provided great encouragement and help at Chillingham (Chillingham Wild Cattle Association). We are extremely grateful to all concerned for their enthusiasm for this project.

Field assistance was also provided, at different points, by Pam Grinter, Andy Howard and Kat Sharrock Walsh (University of Birmingham). Danielle Schreve and Richard Thomas (University of Leicester) proved very adept at fishing dung beetles out of buckets at Chillingham despite having a number of better things to do at the time. Processing of material from both projects was undertaken by Kalla Nayyar, Wendy Smith, Katie Ward (University of Birmingham) and Sarah Davies (now Coulter) and Kerry Allen (Queen's University Belfast). Kalla Nayyar identified the majority of the fauna from the dung pats. This text was proof read by Wendy Smith and the authors. Fig. 1 was prepared by Henry Buglass (University of Birmingham).

The work at Dunham Massey and Epping Forest was funded by NERC (NE/D007577/1, to Whitehouse and Smith), "Fossil insect remains as indicators of the primeval forest; a modern analogue approach". Work at Wildwood, Stodmarsh and Chillingham was funded in part by the Institute for Archaeology and Antiquity and the College of Arts and Law, University of Birmingham. Danielle Schreve would also like to thank the Royal Geographical Society (with the Institute of British Geographers) since this study makes a contribution to RGS Grant 1265.3839 Global Change and Sustainable European Landscape Management Project. The authors are grateful to all institutions for this support.

## References

- Allen, J.R.M., Scouse, J.D., Hall, A.R., Coope, G.R., 2009. Palaeoenvironmental context of the Late-glacial woolly mammoth (*Mammuthus primigenius*) discoveries at Condevor, Shropshire, UK. *Mammalogy Journal* 44, 414–446.
- Atkinson, T.C., Briffa, K.R., Coope, G.R., 1987. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325, 587–592.
- Barbero, E., Palestini, C., Rolando, A., 1999. Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeoidea). *Journal of Insect Conservation* 3, 75–84.
- Buckland, P.I., Buckland, P.C., 2006. BugsCEP Coleopteran Ecology Package. (Version: BUGSCEP 7.63 (Downloaded March 2013) URL: <http://www.bugscep.com>).
- Carpaneto, G.M., Mazziotta, A., Piattella, E., 2005. Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). *Biological Conservation* 123, 547–556.
- Carrott, J., Kenward, H.K., 2001. Species associations amongst insect remains from urban archaeological deposits and their significance in reconstructing the past human environment. *Journal of Archaeological Science* 28, 887–905.
- Coope, G.R., 1961. On the study of glacial and interglacial insect faunas. *Proceedings of the Linnean Society of London* 172, 62–65.
- Coope, G.R., 1973. Tibetan species of dung beetle from Late Pleistocene deposits in England. *Nature* 245, 335–336.
- Coope, G.R., 1977. Fossil Coleoptera assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philosophical Transactions of the Royal Society of London B* 280, 313–340.
- Coope, G.R., 2000. Coleoptera from Beeston and West Runton, Norfolk. In: Lewis, S.G., Whiteman, C.A., Preece, R.C. (Eds.), *The Quaternary of Norfolk & Suffolk*. Quaternary Research Association, London, pp. 73–76.
- Coope, G.R., 2001. Biostratigraphical distinction of interglacial coleopteran assemblages from southern Britain attributed to Oxygen Isotope Stages 5e and 7. *Quaternary Science Reviews* 20, 1717–1722.
- Coope, G.R., 2010. Coleopteran faunas as indicators of interglacial climates in central and southern England. *Quaternary Science Reviews* 29, 1507–1514.
- Coope, G.R., 2012. The insect remains from the Mammoth channel at Lynford, Norfolk. In: Boismier, W.A., Gamble, C., Coward, F. (Eds.), *Neanderthals Amongst Mammoths: Excavations at Lynford Quarry, Norfolk*. English Heritage, London, pp. 75–96.
- Dormont, L., Epinat, G., Lumaret, J.P., 2004. Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. *Environmental Entomology* 33, 370–377.
- Dormont, L., Rapior, S., McKey, D.B., Lumaret, J.-P., 2007. Influence of dung volatiles on the process of resource selection by coprophagous beetles. *Chemoecology* 17, 23–30.
- Elias, S.A., 2010. Advances in Quaternary Entomology. In: *Developments in Quaternary Sciences*, vol. 12. Elsevier, Amsterdam.
- Finn, J.A., Giller, P.S., 2002. Experimental investigations of colonisation by North temperate dung beetles of different types of domestic herbivore dung. *Applied Soil Ecology* 20, 1–13.
- Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B., Robinson, G.S., 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326, 1100–1103.
- Girling, M.A., 1989. Mesolithic and later landscapes interpreted from the insect assemblages of West Heath Spa Hampstead. In: Collins, D., Lorimer, D. (Eds.), *Excavations at the Mesolithic Site on West Heath, Hampstead 1976–1981*, British Archaeological Reports, vol. 217. British Archaeological Reports, Oxford, pp. 72–89.
- Gittings, T., Giller, P.S., 1998. Resource quality and the colonisation and succession of coprophagous beetles. *Ecography* 2, 581–592.
- Hansen, M., 1987. The Hydrophilidae (Coleoptera) of Fennoscandia and Denmark Fauna. In: *Fauna Entomologica Scandinavica*, vol. 18. Scandinavian Science Press, Leiden.
- Hanski, I., 1991. North temperate dung beetles. In: Hanski, I., Cambefort, Y. (Eds.), *Dung Beetle Ecology*. Princeton University Press, Princeton, New Jersey, pp. 75–96.
- Jeffers, E.S., Bonsall, M.B., Watson, J., Willis, K.J., 2012. Climate change impacts on ecosystem functioning: evidence from an Empetrum heathland. *New Phytologist* 193, 150–164.
- Jessop, L., 1986. Coleoptera: Scarabaeidae. In: *Handbooks for the Identification of British Insects* 5/11. Royal Entomological Society of London, London.
- Johnson, C.N., 2009. Ecological consequences of Late Quaternary extinctions of megafauna. *Proceedings Biological Sciences/The Royal Society* 276, 2509–2519.
- Kenward, H.K., 1975. Pitfalls in the environmental interpretation of insect death assemblages. *Journal of Archaeological Science* 2, 85–94.
- Kenward, H.K., 1978. The Analysis of Archaeological Insect Assemblages: a New Approach. In: *Archaeology of York*, 19/1. Council for British Archaeology for York Archaeological Trust, London.
- Kenward, H.K., 1982. Insect communities and death assemblages, past and present. In: Hall, A.R., Kenward, H.K. (Eds.), *Environmental Archaeology in the Urban Context*, Council for British Archaeology Research Report, vol. 43. Council for British Archaeology, London, pp. 71–78.
- Kenward, H.K., 2006. The visibility of past trees and woodlands: testing the value of insect remains. *Journal of Archaeological Science* 33, 1368–1380.
- Kenward, H.K., Hall, A.R., 1995. Biological Evidence from Anglo-scandinavian Deposits at 16–22 Coppergate. In: *The Archaeology of York* 14/7. Council for British Archaeology, London.
- Kenward, H.K., Hall, A.R., 1997. Enhancing bio-archaeological interpretation using indicator groups: stable manure as a paradigm. *Journal of Archaeological Science* 24, 663–673.
- Kenward, H.K., Hall, A.R., Jones, A.K.G., 1980. A tested set of techniques for the extraction of plant and animal macrofossils from waterlogged archaeological deposits. *Science and Archaeology* 22, 3–15.
- Kenward, H.K., Hall, A.R., McComish, J.M., 2004. Archaeological implications of plant and invertebrate remains from fills of a massive Post-Medieval cut at Low Fishergate, Doncaster, UK. *Environmental Archaeology* 9, 61–74.
- Koch, K., 1989. Die Käfer Mitteleuropas (Ökologie Band 2). Goecke and Evers, Krefeld.
- Koskela, H., Hanski, I., 1977. Structure and succession in a beetle community inhabiting cow dung. *Annales Zoologici Fennici* 14, 204–223.
- Lewis, J., Brown, F., Batt, A., Cooke, N., Barrett, J., Every, R., Mephum, L., Brown, K., Cramp, K., Lawson, A.J., Roe, F., Allen, S., Petts, D., McKinley, J., Carruthers, W., Challinor, D., Wiltshire, P., Robinson, M., Lewis, H., Bates, M., 2006. Landscape Evolution in the Middle Thames Valley: Heathrow Terminal 5 Excavations. In: *Perry Oaks (Framework Archaeology Monograph no.1)*, vol. 1. Framework, Oxford and Salisbury.
- Lott, D., 2009. The Staphylinidae. In: *Handbooks for the Identification of British Insects*, vol. 12 part 5. Royal Entomological Society, London.
- Lucht, W.H., 1987. Die Käfer Mitteleuropas (Katalog). Goecke and Evers, Krefeld.
- Mitchell, F.J.G., 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* 93, 168–177.
- Robinson, M.A., 1979. The biological evidence. In: Lambrick, G., Robinson, M.A. (Eds.), *Iron Age and Roman Riverside Settlements at Farmoor, Oxfordshire*, Council for British Archaeology Research Report, vol. 32. Council for British Archaeology, London, pp. 77–133.



- Robinson, M.A., 1981. The use of ecological groupings of Coleoptera for comparing sites. In: Jones, M., Dimbleby, G. (Eds.), *The Environment of Man: The Iron Age to the Anglo-saxon Period*, British Archaeological Reports, British Series, vol. 87. British Archaeological Reports, Oxford, pp. 251–286.
- Robinson, M.A., 1983. Arable/pastoral ratios from insects? In: Jones, M. (Ed.), *Integrating the Subsistence Economy*, British Archaeological Reports, International Series, vol. 181. British Archaeological Reports, Oxford, pp. 19–47.
- Robinson, M., 1993. The Iron Age environmental evidence. In: Allen, T.G., Robinson, M.A. (Eds.), *The Prehistoric Landscape and Iron Age Enclosed Settlement at Mingies Ditch, Hardwick-with-yelford, oxon, Thames Valley Landscapes: The Windrush Valley*, vol. 2. Oxford Archaeological Unit, Oxford, pp. 101–120.
- Robinson, M.A., 2000. Coleopteran evidence for the Elm Decline, Neolithic activity in woodland, clearance and the use of the landscape. In: Fairbairn, A.S. (Ed.), *Plants in Neolithic Britain and beyond*, Neolithic studies group seminar papers, vol. 5. Oxbow Books, Oxford, pp. 27–36.
- Rule, S., Brook, B.W., Haberle, S.G., Turney, C.S.M., Kershaw, A.P., Johnson, C.N., 2012. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science* 335, 1483–1486.
- Schreve, D.C., 2004. *The Quaternary Mammals of Southern and Eastern England*. Field Guide, Quaternary Research Association, London.
- Smith, K.G.V., 1989. An Introduction to the Immature Stages of British Flies. In: *Handbooks for the Identification of British Insects*, vol. 10/14. Royal Entomological Society of London, London.
- Smith, D., 1996. Thatch, turves and floor deposits: a survey of Coleoptera in materials from abandoned Hebridean blackhouses and the implications for their visibility in the archaeological record. *Journal of Archaeological Science* 23, 161–174.
- Smith, D., 1998. Beyond the barn beetles: difficulties in using some Coleoptera as indicators for stored fodder. *The Journal of Environmental Archaeology* 1, 63–70.
- Smith, D.N., 2000. Detecting the nature of materials on farms using Coleoptera. In: Huntley, J.P., Stallibrass, S. (Eds.), *Taphonomy and Interpretation*, AEA Symposia No. 14. Oxbow Books, Oxford, pp. 71–84.
- Smith, D.N., 2002. The insect remains. In: Coates, G.A. (Ed.), *Prehistoric and Romano-British Landscape: Excavations at Whitmoor Haye Quarry, Staffordshire*, 1997–1999, British Archaeological Reports, British Series, vol. 340. British Archaeological Reports, Oxford, pp. 67–72.
- Smith, D., 2011. '[Romano-British] Insect Remains' in Jones Excavations at Little Paxton Quarry, Cambridgeshire, 1992–1998. In: *Birmingham Archaeology Monograph Series 10/British Archaeological Reports B*, vol. 545. British Archaeological Reports, Oxford, pp. 265–277.
- Smith, D.N., Smith, W., 2009. Insect and Plant Remains from the Banbury Centre Redevelopment (University of Birmingham Environmental Archaeology Services Report vol. 115). (Unpublished report to excavator).
- Smith, D., Letts, J.P., Cox, A., 1999. Coleoptera from Late Medieval smoke blackened thatch (SBT): Its archaeological implications. *Environmental Archaeology* 4, 9–18.
- Smith, D.N., Whitehouse, N., Bunting, M.J., Chapman, H., 2010. Can we characterise 'openness' in the Holocene palaeoenvironmental record? Analogue studies from Dunham Massey deer park and Epping Forest, England. *The Holocene* 20, 215–229.
- Svenning, J.-C., 2002. A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104, 133–148.
- Tottenham, C.E., 1954. Coleoptera. Staphylinidae, Section (A) Piestinae to Euaethetinae. In: *Handbooks for the Identification of British Insects*, IV, 8a. Royal Entomological Society, London.
- Vera, F.W.M., 2000. *Grazing Ecology and Forest History*. CABI Publishing, Oxon.
- Welch, R.C., 1997. The British species of the genus *Aleochara* Gravenhorst (Staphylinidae). *Coleopterist* 6, 1–45.
- Weßmer, T., 1995. Selection of the Spatial Habitat of Coprophagous Beetles in the Kaiserstuhl Area Near Freiburg (SW-Germany). *Acta Oecologica* 16, 461–478.
- Weßmer, T., 1994. Seasonality of coprophagous beetles in the Kaiserstuhl area near Freiburg (SW-Germany) including the winter months. *Acta Oecologica* 15, 607–631.
- Whitehouse, N., Smith, D., 2010. How fragmented was the British Holocene wild-wood? Perspectives on the "Vera" grazing debate from the fossil beetle record. *Quaternary Science Reviews* 29, 539–553.
- Whitehouse, N.J., Smith, D.N., Schreve, D., 2013. Long-term perspectives on landscape structure, ecological change and biodiversity during the Quaternary. In: *Book of Abstracts PAGES Goa, 4th Open Science Meeting: the Past Is a Compass for Future Earth*, 12th–16th February 2013, pp. 199–200.